TAXONOMIC STATUS AND RELATIONSHIPS OF THE SWAN ISLAND HUTIA, *GEOCAPROMYS THORACATUS* (MAMMALIA: RODENTIA: CAPROMYIDAE), AND THE ZOOGEOGRAPHY OF THE SWAN ISLANDS VERTEBRATE FAUNA

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Abstract.—Comparisons of external and cranial characters in the three Recent species of *Geocapromys* demonstrate that the Swan Island Hutia, *G. thoracatus,* is a distinct species, rather than a subspecies of the Jamaican Hutia, *G. brownii,* as it has been regarded by most recent authors. Based on derived characters of the zygomatic arch region, *G. thoracatus* and *G. brownii* are closely related and constitute a species-group within *Geocapromys.* The third extant species of the genus, *G. ingrahami* from the Bahamas, and at least four extinct species referable to *Geocapromys* form a second species-group. All available information pertaining to the recent extinction of the Swan Island Hutia is reviewed. Zoogeographic analysis of the Swan Islands vertebrate fauna reveals that the majority of species have been derived from the West Indies, substantiating placement of the Swan Islands in the West Indian Subregion of the Neotropical Region. Overwater dispersal is advocated to explain the origin of the fauna, as the geological history of the Swan Islands precludes vicariance as a tenable biogeographic hypothesis.

"There are some islands which are so small and isolated that the mere presence, or the mere absence, of certain birds and mammals on them, lends them just that touch of interest which they would not otherwise possess." Percy Lowe (1911: 38).

Geocapromys thoracatus, a member of the endemic West Indian hystricognath rodent family Capromyidae, is known only from Little Swan Island, a tiny (2 km²), remote, limestone island located in the northwestern Caribbean Sea. The taxonomic status of *G. thoracatus* has been unclear from the beginning. When True (1888) described *G. thoracatus* as a subspecies of the Jamaican Hutia, *Capromys brachyurus* Hill, 1851 (=*C. brownii* Fischer, 1830), he compared only external characteristics of the two forms. Jamaican specimens were not available to True, so his comparisons were based on Hill's original description of *C. brachyurus* in Gosse (1851). True (1888:470) distinguished *thoracatus* from *brachyurus* on the basis of ". . . the white band of fur across the breast, the gray throat, and brown and ochreous (not blackish) hind feet . . . ." He noted that the Little Swan specimens, of which he had two, closely resembled *C. brachyurus* in size and proportions. This last observation is puzzling, because all later workers have mentioned the considerably larger size of the Jamaican animal.

In his original description of *Capromys ingrahami* from East Plana Cay, a small island in the Crooked-Acklins group in the south-central Bahamas, J. A. Allen (1891) compared the species with *C. thoracatus.* He noted that these two species

were similar in overall coloration, but that *C. ingrahami* was a smaller animal with a relatively longer tail, and also differed in cranial features. Except for the narrower jugal and less pronounced lateral jugal fossa of *C. ingrahami,* most of Allen's characters are of doubtful value as judged from larger samples.

Chapman (1901), in his revision of *Capromys,* erected the subgenus *Geocapromys* to include the short-tailed members of the genus: *G. brownii, G. thoracatus,* and *G. ingrahami.* Compared with the other two species, Chapman found that the skull of *G. brownii* is larger, lacks supraorbital processes and is relatively broader at the interorbital constriction. In a direct comparison of *G. brownii* and *G. thoracatus,* Chapman (1901:321) made the following observations: "The acquisition of the above-mentioned specimen of *C. brownii* (=*brachyurus* auct.) permits, for the first time, actual comparison of *thoracatus* with the form to which it has generally been supposed to be subspecifically related. The result shows the two animals to differ widely from each other in color, dimensions, particularly of the ears, and in cranial characters. In fact, *thoracatus* proves to be much more closely related to *ingrahami,* from which indeed it is to be distinguished externally only by size, the two known specimens of *thoracatus* agreeing exactly in color with the prevailing type of *C. ingrahami* as it is shown by a series of twelve specimens in the America Museum." Based on the differences between *G. brownii* and *G. thoracatus,* Chapman regarded the latter as a full species.

G. M. Allen elevated *Geocapromys* to generic rank and in so doing, he noted (1917:8–9), "Three living species are included in this genus. Of these, *Geocapromys brownii,* of Jamaica, is the largest. The two others, *G. thoracatus* of Little Swan Island, and *G. ingrahami* of Plana Keys, Bahamas, are smaller, and much more resemble each other in their gray type of coloring than they do the large dark brown animal of Jamaica. As Chapman pointed out, these may indicate two species groups." Allen also mentioned that the incisors are very pale yellow in *G. brownii* and *G. ingrahami* and ivory white in *G. thoracatus*; however, every specimen of *G. brownii* I have examined has dark, yellowish-orange incisors.

In a report on the generic characters of *Geocapromys,* Miller (1929) noted that the ascending process of the maxilla is essentially vertical in *G. ingrahami* and posteriorly sloping in *G. brownii* and *G. thoracatus.* Lawrence (1934) presented a key summarizing the cranial characters of all the then known species of *Geocapromys,* both living and extinct. She distinguished *G. brownii* based on its larger size, anterior inflation of the frontals, constriction of the frontals posterior to the supraorbital processes, and short, bluntly triangular supraorbital processes. *Geocapromys thoracatus* was differentiated from *G. brownii* by its smaller size and from *G. ingrahami* by the pronounced jugal spine and more vertical posterior margin of the jugals.

Geocapromys thoracatus was recognized as a distinct species from the time Chapman (1901) first accorded it full specific rank until Mohr (1939) relegated it to its current status as a subspecies of *G. brownii.* Almost all authors have followed Mohr in calling the Swan Island Hutia, *G. brownii thoracatus* (Clough 1972, 1976; Hall 1981; Oliver 1976, 1977; Varona 1974). Furthermore, Mohr (1939) reduced *Geocapromys* to its former status as a subgenus of *Capromys,* a usage that has gained favor with some recent authors (Hall 1981; Varona 1974). However, based on nine external and cranial characters, I recognize *Geocapromys* as a distinct genus. External features which differentiate *Geocapromys* from *Capromys* are the

short tail, reduced first digit on the front foot, and the shorter, finer fur. Cranial characters separating the two genera are discussed in detail by Morgan (1977) and Woods and Howland (1979). The most significant diagnostic features of *Geocapromys* noted by these authors are: the less arched or more procumbent incisors, the origin of the upper incisor root capsule high on the maxilla above the P^4, the broad vertically or posteriorly oriented superior zygomatic root of the maxilla, the tendency toward anterior convergence of the upper tooth rows, the labial inclination of the occlusal surface of the cheek teeth, and the presence of an additional anterolingual re-entrant (anteroflexid) on the P_4.

In a study of the living and extinct species of *Geocapromys* undertaken to determine the affinities of an undescribed extinct species of the genus from the Cayman Islands (Morgan 1977), it became clear to me that the external and cranial differences between *G. thoracatus* and *G. brownii* represented distinctions between species, not subspecies. Many of these differences have been pointed out by previous authors, but they have not been adequately summarized. For the sake of completeness, I have included *G. ingrahami* in my descriptions and analyses.

Methods and specimens.—External measurements are those of the original collectors and were taken from skin labels. Cranial measurements were taken with dial calipers and rounded to the nearest 0.1 mm. In addition to the standard mammalian cranial measurements, as defined in DeBlase and Martin (1974), other measurements were taken. Those that require further explanation include: the internal width of palate taken between the anterolingual edges of alveoli of P^4 and M^1 and at the posterior palatal margin; the occlusal lengths of the upper and lower tooth rows are measurements of the teeth—not alveoli; length of dentary taken from posterior tip of angular process to anterior extension of incisor alveolus; and length of mandibular symphysis taken from posterior edge of alveolar sheath to anterior extension of incisor alveolus. Only adults were measured, as determined by the eruption and wear on M_3^3 and by fusion of the basioccipital and basisphenoid. For two reasons the sexes were combined in the statistical analyses. First, the sex was not recorded on 25 of the 65 specimens examined. Second, the presence of an enlarged clitoris in female *Geocapromys* increases the likelihood that individuals were incorrectly sexed in the field. For example, of the 25 sexed specimens of *G. thoracatus* and *G. ingrahami* examined, only three were recorded as females. Descriptive morphological terms are standard except certain terms used to describe hystricognathous rodents (Woods and Howland 1979). Dental terminology follows Wood and Patterson (1959:287).

I examined and measured the majority of existing specimens of Recent *Geocapromys,* including all specimens from the following museums: American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Florida State Museum (UF), Museum of Comparative Zoology (MCZ), and National Museum of Natural History, Smithsonian Institution (USNM). The following specimens were examined:

Geocapromys brownii (23; 9 ♂♂, 6 ♀♀, 8?) JAMAICA: Portland Parish, John Crow Mountains, AMNH (7), MCZ (2), UF (1); Stony Hill, UF (1); St. Thomas Parish, Cuna Cuna, AMNH (1), MCZ (1), USNM (2); St. Catherine Parish, Worthy Park, UF (2); no specific locality, AMNH (2), BMNH (2), MCZ (3).

Geocapromys ingrahami (21; 9 ♂♂, 1 ♀, 11?) BAHAMAS, East Plana Cay, AMNH (8, including type), BMNH (2), MCZ (8), USNM (3).

Geocapromys thoracatus (21; 13 ♂♂, 2 ♀♀, 6?) SWAN ISLANDS, Little Swan Island, AMNH (2), BMNH (7), MCZ (10), USNM (2, including type).

Morphological Comparisons

External characters. — The most obvious difference among the three species of *Geocapromys* is size (Table 1): *G. brownii* is largest in body size, *G. thoracatus* is intermediate, and *G. ingrahami* is smallest. As noted by many previous workers, *G. thoracatus* and *G. ingrahami* are similar in overall coloration. Both species have grayish-brown upperparts and a light brown to tan venter. In these two species, the majority of hairs on the back are light brown at the base with tan tips, but interspersed with these, especially in the middle of the back, are longer unbanded dark brown hairs. These darker hairs, together with the paler banded hairs, produce the grayish-brown color of the dorsum. *Geocapromys thoracatus* has a cream-colored collar 1–3 cm in width that extends transversely across the chest between the front limbs, hence the specific epithet. *Geocapromys ingrahami* lacks this bar, but some individuals do have a cream-colored spot between the front limbs that may extend posteriorly to the genital region. Compared to the two smaller species, *G. brownii* is a much darker animal, being dark reddish-brown to blackish-brown on the dorsum and medium brown on the belly. The dorsal guard hairs are alternately banded reddish-brown and dark brown or black, with longer black hairs interspersed. Unlike the other two species, *G. brownii* has no lighter colored spots or bars on the underside.

The tail is short in all *Geocapromys,* but it varies among the three species (Table 1). The tail is shorter than the hind foot and sparsely furred in *G. brownii,* approximately equal in length to the hind foot and sparsely furred in *G. thoracatus,* and longer than the hind foot and densely furred with short, reddish-brown hairs in *G. ingrahami.* The difference in tail length between the three species appears to be correlated with the number of caudal vertebrae. The longest-tailed species, *G. ingrahami,* has an average of 19 caudal vertebrae, *G. thoracatus* has 17, and *G. brownii* 14.

The ears also differ in size (Table I) and morphology among the living members of the genus. *Geocapromys thoracatus* has comparatively large ears that appear to be almost naked, although both the internal and external surfaces have a sparse covering of short, fine hairs. *Geocapromys brownii* has small ears that are covered by a dense mat of short, fine hairs and in addition has two tufts of longer hair on the inner surface of the pinna, one above and behind the meatus and the other directly posterior to the meatus on the ventrolateral margin of the ear. *Geocapromys ingrahami* has intermediate-sized ears that are clothed with long, posteriorly directed hairs. As in *G. brownii,* there are two tufts of hair along the inner dorsal margin of the ear, although the tufts are much more prominent in *G. ingrahami.* The presence of long ear tufts in *G. ingrahami* appears to be unique within the Capromyidae. Most species of *Capromys* have nearly naked ears, resembling those of *G. thoracatus.*

Cranium. — The most obvious difference between the cranium of *Geocapromys brownii* on the one hand and *G. thoracatus* and *G. ingrahami* on the other, is the larger size of the former (Table 1, Figs. 1, 2). *Geocapromys brownii* averages 15–

Table 1.—External, skull, and dental measurements (in mm) of *Geocapromys brownii, G. thoracatus,* and *G. ingrahami.* The mean, standard deviation, sample size (in parentheses), and observed range, respectively, are given for each measurement.

Measurement	*Geocapromys brownii*	*Geocapromys thoracatus*	*Geocapromys ingrahami*
Length of head and body	410 ± 24 (12) 372–448	338 ± 4 (5) 334–343	308 ± 21 (4) 280–326
Length of tail	48 ± 8 (13) 40–64	65 ± 5 (5) 57–70	77 ± 5 (7) 70–85
Length of hindfoot	70 ± 6 (14) 60–78	66 ± 2 (5) 64–70	58 ± 5 (7) 53–65
Length of ear (from notch)	20 ± 1 (5) 19–21	26 ± 1 (8) 24–28	19 ± 4 (7) 15–24
Number of caudal vertebrae	14 ± 1 (7) 12–15	17 ± 1 (8) 15–18	19 ± 1 (5) 18–19
Greatest length of skull	81.1 ± 3.7 (19) 75.1–87.0	68.6 ± 1.8 (19) 65.9–73.0	63.2 ± 1.2 (16) 61.5–65.6
Condylobasal length	75.3 ± 4.0 (14) 68.9–81.6	63.6 ± 2.0 (18) 60.4–67.9	59.3 ± 1.4 (12) 57.5–61.6
Zygomatic breadth	43.7 ± 2.5 (18) 39.1–48.4	34.8 ± 1.3 (18) 32.7–36.9	32.8 ± 1.3 (18) 30.3–34.9
Breadth at auditory meatus	29.5 ± 1.1 (17) 27.2–30.9	25.0 ± 0.9 (17) 23.4–27.1	24.4 ± 1.0 (15) 23.2–26.5
Breadth of frontals anterior to supraorbital processes	23.9 ± 1.2 (18) 20.5–26.1	17.8 ± 0.8 (21) 16.3–19.3	17.1 ± 0.8 (19) 15.3–18.5
Breadth of frontals posterior to supraorbital processes	19.7 ± 1.2 (19) 18.0–22.6	19.9 ± 0.8 (21) 18.8–21.3	17.9 ± 0.7 (19) 17.1–19.3
Breadth of superior zygomatic root of maxilla	5.5 ± 0.9 (19) 4.0–7.6	4.5 ± 0.3 (20) 4.0–5.2	3.2 ± 0.6 (18) 1.9–4.3
Breadth of palate anterior to P^4	3.4 ± 0.5 (18) 2.6–4.2	2.6 ± 0.3 (21) 2.3–3.1	2.4 ± 0.3 (19) 1.9–2.8
Breadth of palate between P^4 and M^1	3.4 ± 0.6 (16) 2.4–4.6	2.9 ± 0.3 (19) 2.3–3.7	2.2 ± 0.3 (19) 1.6–2.8
Breadth of palate at posterior palatal margin	6.4 ± 0.4 (18) 5.5–7.0	5.6 ± 0.3 (19) 5.3–6.5	4.8 ± 0.4 (19) 3.8–5.6
Length of upper diastema	19.6 ± 1.1 (19) 17.9–21.6	17.0 ± 0.6 (20) 16.0–18.5	15.4 ± 0.5 (18) 14.7–16.6
Alveolar length of upper tooth row	19.3 ± 0.7 (19) 18.0–20.3	15.2 ± 0.5 (21) 14.4–15.9	15.6 ± 0.5 (19) 14.8–16.4
Occlusal length of upper cheek teeth	18.1 ± 0.7 (11) 17.0–19.4	14.1 ± 0.6 (21) 12.8–15.4	14.6 ± 0.6 (18) 13.3–15.6
Greatest length of mandible	55.8 ± 2.7 (17) 50.7–59.8	45.2 ± 1.6 (18) 41.4–48.3	41.3 ± 1.7 (15) 38.0–43.2
Length of lower diastema	13.7 ± 1.0 (19) 12.6–16.0	12.8 ± 0.7 (20) 11.5–14.3	10.1 ± 0.6 (18) 9.2–11.3
Alveolar length of lower tooth row	19.1 ± 1.0 (19) 17.5–21.0	14.6 ± 0.5 (20) 13.3–15.4	15.2 ± 0.6 (17) 13.9–16.2
Occlusal length of lower cheek teeth	18.7 ± 1.0 (12) 17.3–20.8	14.4 ± 0.6 (20) 13.5–15.5	14.6 ± 0.6 (17) 13.7–15.6

20% larger than *G. thoracatus,* depending on the measurement, with almost no overlap between the smallest *G. brownii* and the largest *G. thoracatus. G. ingrahami* is slightly smaller (6–8%) than *G. thoracatus,* but there is broad overlap between them in some measurements.

One of the most characteristic features of *Geocapromys brownii* is the prominent inflation of the frontals medial to the anterior edge of the orbits. The degree of frontal inflation varies individually, but all show some evidence of it. When viewed laterally, the frontals are seen to form a noticeable bulge in the dorsal profile of the skull (Fig. 1D). The inflation of the frontal sinuses begins immediately posterior to the nasofrontal suture, extends posteriorly to the level of the supraorbital processes, and is also present on the orbital wall dorsal to the lacrimals. The frontals are not inflated in *G. thoracatus* or *G. ingrahami.* Although the functional significance of frontal inflation is not known, it is present in several other groups of hystricognath rodents, particularly in the porcupines *Coendou* and *Hystrix.* Anterior to the frontoparietal suture, the interorbital region is strongly constricted in *G. brownii,* but not in the other two species. The anteriorly inflated and posteriorly constricted frontals of *G. brownii* are thus considerably broader anterior to the supraorbital processes than posterior to them. This contrasts with *G. thoracatus,* in which the frontals are always broader posterior to the supraorbital processes, and with *G. ingrahami,* in which the two measurements are nearly equal.

Most specimens of *Geocapromys brownii* have a moderate to strongly developed sagittal crest formed by the convergence of weak temporal crests. The temporal crests are stronger in *G. thoracatus* and *G. ingrahami,* but never meet to form a sagittal crest in the latter, and only rarely meet to form a weak crest in the former. Compared to the other two species, *G. ingrahami* has an inflated and foreshortened braincase and a constricted pterygoid region. The auditory bullae of *G. ingrahami* are also inflated, whereas those of *G. brownii* and *G. thoracatus* are not. In posterior view, the bullae of *G.ingrahami* project ventral to the occipital condyles, whereas in the other two species the ventral surface of the bullae is always dorsal to the condyles. Additionally, the bullae of *G. ingrahami* are comparatively shorter, broader anteriorly, and have a larger external auditory meatus. The combination of the inflated bullae and a narrower basioccipital results in the anterior portions of the bullae being in closer approximation in *G. ingrahami* than in its congeners.

In all *Geocapromys,* the lateral jugal fossa is present, being particularly large in *G. brownii,* slightly smaller in *G. thoracatus,* and reduced in *G. ingrahami.* The enlarged jugal fossa of *G. brownii* is partially the result of a prominent jugal spine on the posteroventral edge of the jugal. The jugal spine is present, but smaller in *G. thoracatus* and absent in *G. ingrahami.* In lateral view, the posterior portion of the zygomatic arch appears to be rotated ventrally in *G. brownii* and *G. thoracatus* in comparison to that of *G. ingrahami* or *Capromys.* The downturning or flexion of the zygomatic arch region is best observed in the relationship between the ventral border of the jugal and the alveolar margin of the upper cheek teeth. The ventral border of the zygomatic arch is inclined relative to the alveolar margin

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Fig. 1.   Dorsal (A–C) and left lateral (D–F) views of cranium of *Geocapromys* species. A, D, *G. brownii,* MCZ 11040, Jamaica; B, E, *G. thoracatus,* AMNH 34547, Little Swan Island; C, F, *G. ingrahami,* MCZ 29427, East Plana Cay, Bahamas. All photographs are natural size.
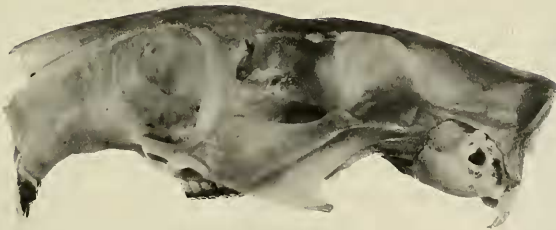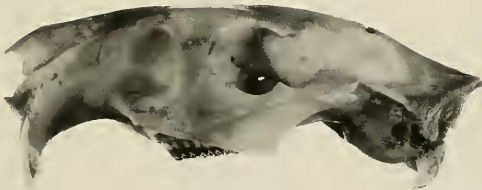
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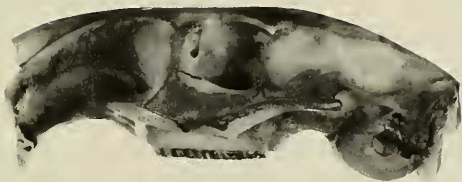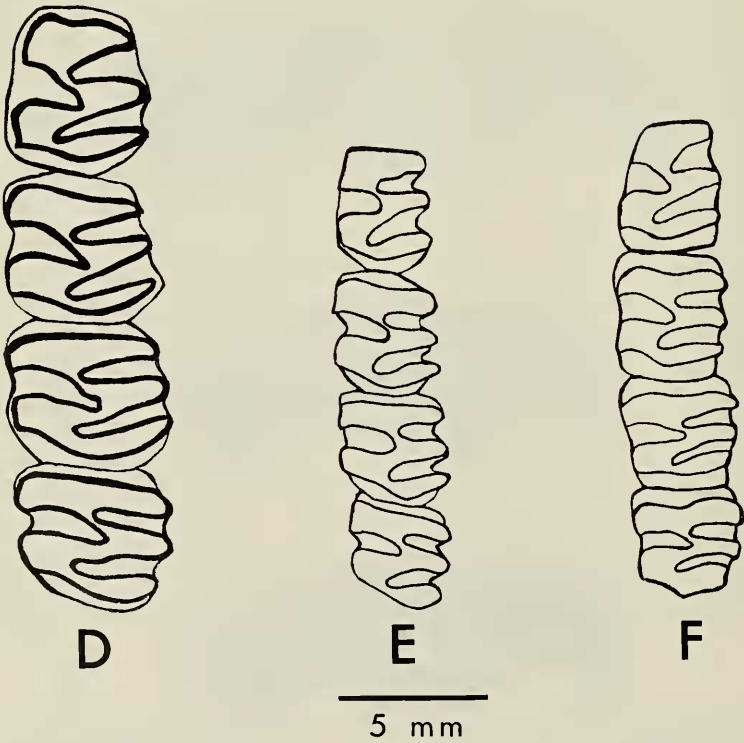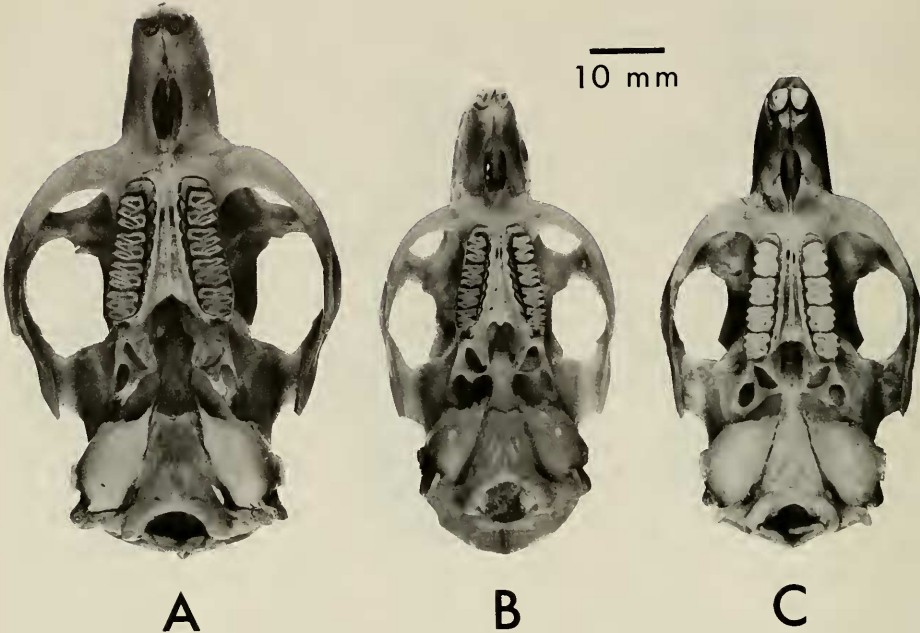
and projects ventral to it in *G. brownii* and *G. thoracatus*. In most specimens of these two species the jugal spine, the ventralmost portion of the zygomatic arch, is ventral to the occlusal surface of the cheek teeth. In *G. ingrahami*, the ventral border of the zygomatic arch is essentially parallel to the alveolar margin and does not project ventral to it. Apparently, as a result of the ventral rotation of the zygomatic arch, the superior zygomatic root of the maxilla in *G. brownii* and *G. thoracatus* is inclined posteriorly relative to a perpendicular line drawn through the alveolar margin. In addition, the superior zygomatic root in these two species is relatively broader than in *G. ingrahami* or *Capromys*. The superior zygomatic root of *G. ingrahami* is perpendicular or inclined slightly anteriorly. The zygomatic arches in *G. brownii* are broadest anteriorly, whereas in *G. thoracatus* and *G. ingrahami* the lateral margins of the zygomatics are parallel.

The upper tooth rows converge anteriorly in all *Geocapromys* more so than in *Capromys*. *Geocapromys ingrahami* shows the greatest tendency toward this convergence, *G. brownii* the least. The upper tooth rows of *G. ingrahami* do not diverge as strongly as in *G. brownii* and *G. thoracatus* and as a result, the internal nares are constricted laterally. The anterior convergence of the upper tooth rows and constriction of the internal nares are carried to an extreme in several extinct species of *Geocapromys* in which the tooth rows nearly meet anteriorly. In contrast to the condition in *G. ingrahami*, the opening of the internal nares is constricted vertically in *G. thoracatus* due to the dorsal inclination of the palate from anterior to posterior. The median ridge of the palate has been used to distinguish species of *Geocapromys*, but I found this character to be highly variable in all species except *G. thoracatus*. *Geocapromys thoracatus* has a small spinous process that projects 1–2 mm beyond the posterior palatal margin along the midline; this process was not observed in any other species of the genus. Both the alveolar and occlusal lengths of the upper tooth rows are shorter in *G. thoracatus* than in *G. ingrahami*, even though the former is larger in most other cranial measurements. This derives from the comparatively small cheek teeth of *G. thoracatus*, a feature discussed in greater detail in the Dentition section.

Mandible.—The coronoid process is triangular and vertical in *Geocapromys thoracatus* and *G. ingrahami*, whereas in *G. brownii* the tip of the coronoid is curved posteriorly. The masseteric crest is broad and rounded laterally in *G. thoracatus*, but is narrower in *G. brownii* and *G. ingrahami*. The pterygoid shelf of the angular process is also broader in *G. thoracatus*. The articular surface of the condyloid process is anteroposteriorly elongate in *G. brownii* and *G. ingrahami*, but is nearly circular in *G. thoracatus*. A postcondyloid process is well developed in *G. brownii*, somewhat smaller in *G. ingrahami*, and reduced in *G. thoracatus*. As in the upper cheek teeth, the lower teeth in *G. thoracatus* are shorter and narrower than in the other species and consequently, the alveolar and occlusal lengths of the tooth rows are shorter. The mandibular tooth rows are closer in *G. ingrahami* than in the other two species, but are not as convergent

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Fig. 2.   Ventral views of cranium (A–C) and occlusal outlines of maxillary cheek teeth (D–F) of *Geocapromys* species. A, D, *G. brownii,* MCZ 11040, Jamaica; B, E, *G. thoracatus,* AMNH 34547, Little Swan Island; C, F, *G. ingrahami,* MCZ 29427, East Plana Cay, Bahamas. Photographs of crania (A–C) are natural size, occlusal outlines of cheek teeth (D–F) are 4× natural size.
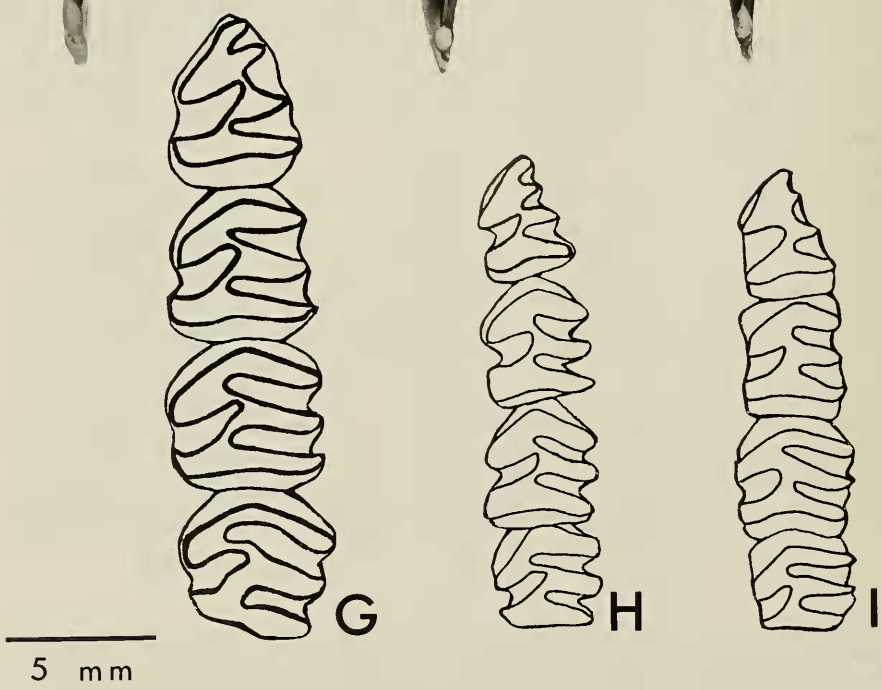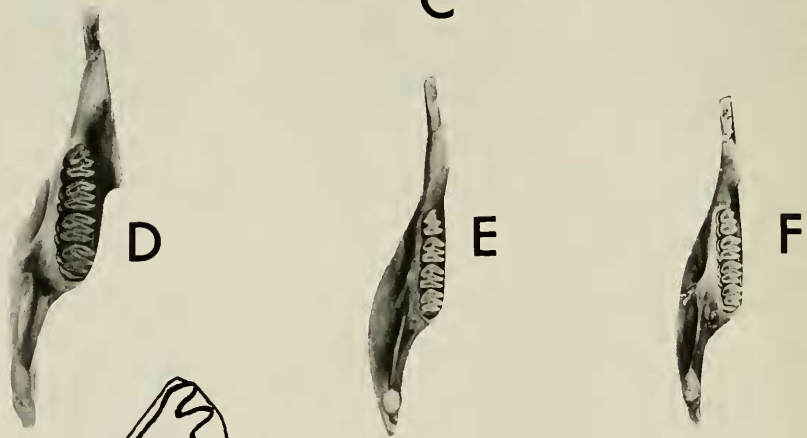
as are their upper counterparts. *Geocapromys ingrahami* has a relatively shorter diastema than do the other two species.

Dentition.—In the cheek teeth of *Geocapromys,* cement is present on that portion of the crown not enclosed by the continuous enamel band, except on the anterior margin of P^4 and the posterior margin of M_3. However, the cement is reduced on all cheek teeth of *G. thoracatus* in comparison to its congeners. In particular, the cement in *G. thoracatus* is thin on the anterior edge of P_4 and absent from the anterolingual edges of M_1-M_3 and the posterolabial edges of P^4-M^2. The edges of the labial lophs and lingual lophids on the upper and lower molars respectively, are more prominent in *G. thoracatus* because the flexi and flexids are not filled entirely to their margins with cement as they are in *G. brownii* and *G. ingrahami.* The thinner layer of cement on the anterior and posterior margins of the cheek teeth in *G. thoracatus* almost certainly accounts for the shorter tooth row lengths observed in this species.

The presence of a small anterolingual re-entrant (anteroflexid) on P_4 is characteristic of all *Geocapromys.* This may be a primitive character, as an anteroflexid or anterofossetid on P_4 is found in echimyids, the presumed sister group of the capromyids. However, the presence of an incipient anteroflexid in some specimens of *Capromys pilorides* indicates that the anteroflexid of *Geocapromys* may be secondarily derived from the condition found in *Capromys* and hence, not strictly homologous with the flexid located in the same position in echimyids. Whether the anteroflexid on P_4 is a primitive character or a neomorph, its morphology differs among the species of *Geocapromys* and is useful in distinguishing them. In *G. brownii,* the anteroflexid is well developed, extending to the midline of P_4 in most specimens and separating the anterolophid into two parts. The medial lingual re-entrant (mesoflexid) nearly contacts the hypoflexid. The posterolingual re-entrant (metaflexid) contacts or nearly contacts the posterior enamel band of the hypoflexid. The anteroflexid is well developed in *G. thoracatus,* but it does not extend to the midline of P_4, nor does it appear to separate the anterolophid into two distinct lophids. The mesoflexid and metaflexid are as in *G. brownii,* except that the metaflexid never distorts the posterior margin of the hypoflexid as it does in some specimens of *G. brownii.* The anteroflexid is invariably present in *G. ingrahami* but it is very small compared to that in the other two species. The mesoflexid of *G. ingrahami* is broad and shallow. The metaflexid extends farther lingually than the mesoflexid, but does not contact the hypoflexid.

The differences in the upper dentition between the species of *Geocapromys* are not as pronounced as in the lowers. The paraflexus and hypoflexus of all upper cheek teeth in *G. brownii* and *G. thoracatus* are in contact along the longitudinal midline, effectively isolating the protoloph. This is also true of the upper molars in *G. ingrahami,* but the paraflexus and hypoflexus are not in contact on P^4.

Color of the incisors has been used in the past to distinguish species of *Geocapromys.* This character must be used with care because a change in incisor

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Fig. 3.   Lateral (A–C) and occlusal (D–F) views of left mandible and occlusal outlines of mandibular cheek teeth (G–I) of *Geocapromys* species. A, D, G, *G. brownii,* MCZ 11040, Jamaica; B, E, H, *G. thoracatus,* AMNH 34547, Little Swan Island; C, F, I, *G. ingrahami,* MCZ 29431, East Plana Cay, Bahamas. Photographs of mandibles (A–F) are natural size, occlusal outlines of cheek teeth (G–I) are 4× natural size.

coloration can result from certain preparation techniques or from long submersion in preservative fluids. Still, there is a consistent difference in incisor color between *G. brownii,* in which the incisors are almost always bright yellowish-orange and *G. thoracatus* and *G. ingrahami* in which the incisors are pale yellow or cream-colored.

Relationships of the Recent species of Geocapromys. — The three Recent species of *Geocapromys* can be readily distinguished from one another on the basis of external, cranial, and dental features. In addition, there are four or five extinct species in the genus, several of which are as distinctive as the Recent species. Three extinct species of *Geocapromys* have been described from Cuba, an undescribed species is known from cave deposits in the Cayman Islands, and fossils of an undetermined number of forms have been recovered from nine of the Bahama Islands. Because of the large number of *Geocapromys* fossils known, I am postponing a detailed discussion of the intrageneric relationships to a future paper reviewing the extinct species. Although the evolutionary history of *Geocapromys* is incomplete without inclusion of the fossils, it seems appropriate to discuss several characters that separate the Recent species into distinct lineages or species-groups, as these will prove useful when the fossil taxa are considered.

Before discussing the relationships within *Geocapromys,* it is necessary to review briefly the broader affinities of the genus in order to establish my criteria for the determination of primitive and derived character states. The Echimyidae and Capromyidae are closely related based on several shared derived characters: the presence of a lateral process of the supraoccipital, the presence of a lateral jugal fossa, and the retention of dP$_4^4$. These and other cranial and dental features suggest strongly that echimyids are the mainland group from which capromyids were derived. Compared to echimyids, capromyids are derived in the possession of high-crowned, rootless, and evergrowing cheek teeth; the presence of cement on the tooth crowns; the absence of a metaloph/metalophid on all cheek teeth; and prominent paraoccipital processes that stand apart from the bullae. *Capromys* resembles echimyids and differs from *Geocapromys* in the possession of a long, well-furred tail; thin, anteriorly oriented superior zygomatic root of the maxilla; narrow jugal; relatively large orbit; and more highly arched, nonprocumbent incisors. Based on the widespread occurrence of these characters in the Echimyidae and other capromyids, they are considered primitive in *Capromys.* In the following analysis, the presence of a particular character in echimyids and *Capromys* would be the basis for regarding that structure as primitive in *Geocapromys.* Similarly, a character present in one or more species of *Geocapromys,* but not in *Capromys* or echimyids, would be considered derived.

Geocapromys brownii is derived relative to its congeners, *Capromys,* and echimyids in several cranial features, including the inflated frontal sinuses, the posterior constriction of the frontals, the well developed sagittal crest, and the anteriorly broadened zygomatic arches. Derived features of *G. thoracatus* are the dorsally sloping palate, the vertical constriction of the internal nares, the posterior palatal spine, and the relatively small teeth. *Geocapromys brownii* and *G. thoracatus* share a unique complex of derived characters in the zygomatic arch region. These include the broad, posteriorly oriented superior zygomatic root, deeper jugal, smaller orbit, and ventral rotation of the entire zygomatic arch. Based on these derived features, *G. brownii* and *G. thoracatus* appear to represent a lineage distinct from other *Geocapromys* species and are here designated the *brownii*

species-group. The close relationship of these two forms is not surprising considering that most recent workers have regarded them as conspecific.

Geocapromys ingrahami is distinguished from *G. brownii* and *G. thoracatus* by its shortened, inflated braincase, constricted pterygoid region, incipiently convergent upper tooth rows, lateral constriction of the internal nares, and inflated auditory bullae. Within the Capromyidae these characters are all derived. *Capromys nanus* also has a shortened, swollen braincase and inflated bullae, but is clearly not closely related to *G. ingrahami* and appears to have developed these features independently. The extinct taxa of *Geocapromys* from Cuba, the Bahamas, and the Cayman Islands possess most of the derived characters present in *G. ingrahami,* although the expression of these characters varies significantly between species. My preliminary analysis of these extinct forms indicates that they are most closely related to *G. ingrahami* and are here grouped with the latter in the *ingrahami* species-group of *Geocapromys* species.

Extinction of the Swan Island Hutia. — From the time of its discovery in 1887 by Charles Townsend, the naturalist aboard the U.S. Fish Commission Steamer *Albatross,* until its extinction less than a century later, *Geocapromys thoracatus* was known to occur only on Little Swan Island. Even though Great Swan Island is less than 0.5 km west of Little Swan, is larger, and supports a more luxuriant vegetation, there is no evidence that the hutia ever occurred there. This is analogous to the situation in the Bahamas where *G. ingrahami* lives in large numbers on East Plana Cay, but has never been found on West Plana Cay, an island of similar size only 3 km to the west (J. A. Allen 1891; Clough 1972). Clough and Fulk (1971) do note that there is very little exposed limestone on West Plana Cay compared to East Plana Cay. The coral rock on West Plana Cay is covered by soil and supports a thicker, higher vegetation than does the eastern island. Most of the limestone in the central portion of Great Swan Island is also soil-covered, whereas Little Swan is almost totally devoid of soil. No species of *Geocapromys* is known to dig its own burrows; instead they live in natural cavities, especially small caves and solution holes in limestone karst areas. It seems probable that Great Swan Island and West Plana Cay are unsuitable for hutias because these islands lack large areas of exposed limestone and the myriad of caves and solution holes which are the inevitable result of the chemical weathering of a limestone terrain in the West Indies. This hypothesis has some corroboration in the distribution of *G. brownii* in Jamaica, where it occurs primarily in areas where there are extensive limestone outcrops.

Naturalists in the early part of this century found hutias to be extremely abundant on Little Swan Island. Lowe (1911:114) ". . . saw at least a dozen others [in addition to the two he had already captured] running about and bolting into the big crevasses with which the island is seamed." George Nelson collected 15 Swan Island Hutias for the Museum of Comparative Zoology in March and April of 1912. Even Lord Moyne, who was the last person to collect *Geocapromys thoracatus,* found hutias so abundant on Little Swan in 1937 that (Moyne 1938:82) ". . . four men from the western island with neither nets nor traps caught twelve alive for us in about two hours." Based on this evidence *G. thoracatus* must have become extinct extremely rapidly, as it was last seen alive sometime in the early 1950's. The Swan Islands suffered a devastating hurricane in 1955, and in the late 1950's or early 1960's a box of unwanted cats was released on Little Swan (Clough 1976). The combination of these two events undoubtedly resulted in the

Fig. 4.   Outline map of western Caribbean Sea showing all islands and mainland areas mentioned in text. Inset in lower right hand corner is enlarged map of Swan Islands.

demise of the Swan Island Hutia. Stewart (1962) and his crew did not find hutias on Little Swan in 1960, nor did they see any of their previously omnipresent fecal pellets. Ronald Crombie and Stephen Busack spent two days on Little Swan in February 1974 collecting reptiles for the Smithsonian Institution, but saw no hutias or fecal pellets (R. I. Crombie, pers. comm.). Garrett Clough and Robert Howe (Clough 1976) spent five days on Little Swan in July and August of 1974 specifically looking for *G. thoracatus* or evidence of its existence there. No hutias or fecal pellets were found and a weathered skull served as the only testimony that the species had ever occurred on the island. Taking into account the great abundance of hutias seen on Little Swan Island by earlier visitors and the total lack of evidence of their existence there after 1960, it appears almost certain that *G. thoracatus* is extinct.

Zoogeography of the Swan Islands.—The Swan Islands are among the most isolated islands in the West Indies. They are located at 17°24′N latitude and 83°56′W longitude, approximately 180 km north of the nearest point on the Middle American mainland and 350 km southwest of Grand Cayman, the closest island in the West Indies (Fig. 4). The Swan Islands lie atop an isolated rise on the southern wall of the Cayman Trench, a deep submarine trench that separates the Swan Islands, Nicaraguan Plateau, and Jamaica on the south from the Cayman Ridge (including the Cayman Islands) and Cuba on the north. After the middle Miocene, localized vertical uplift raised the Swan Islands near or above sea level, while the surrounding crust subsided (Perfit and Heezen 1978). Since the late

Table 2.—Zoogeographic affinities of the Swan Islands vertebrate fauna.

Species	General affinities	Specific affinities
Reptilia[1]		
Ameiva ameiva fuliginosa	Middle America	Isla de Providencia
*Anolis sagrei nelsoni	indeterminate	indeterminate
*Aristelliger praesignis nelsoni	West Indies	Jamaica and Cayman Islands
Cnemidophorus l. lemniscatus	Middle America	indeterminate
Iguana iguana	Middle America	indeterminate
Leiocephalus carinatus varius	West Indies	Cayman Islands
*Sphaerodactylus notatus exsul	West Indies	Cuba
*Alsophis cantherigerus brooksi	West Indies	Cuba and Cayman Islands
Leptotyphlops goudoti magnamaculata	Middle America	Isla de Providencia and Isla San Andres
Aves[2]		
Sula l. leucogaster	indeterminate	indeterminate
Sula s. sula	indeterminate	indeterminate
Fregata magnificens	indeterminate	indeterminate
Columba leucocephala	West Indies	indeterminate
Coccyzus minor nesiotes	West Indies	Jamaica and Cayman Islands
Crotophaga ani	West Indies	indeterminate
Mimocichla plumbea rubripes	West Indies	Cuba
*Dendroica vitellina nelsoni	West Indies	Cayman Islands
Mammalia		
†Geocapromys thoracatus	West Indies	Jamaica

* Endemic subspecies.
† Endemic species.
[1] Data from MacLean *et al.* (1977) and Schwartz and Thomas (1975).
[2] Data from Paynter (1956).

Miocene they have existed as either low islands or shallow carbonate banks. Depths in excess of 2000 m are encountered within 30 km of the Swan Islands in any direction. Based on these profound depths and the rates of subsidence for the surrounding ocean floor over the past 20 million years (Perfit and Heezen 1978), it appears that the Swan Islands have never been connected to other land. However, during periods of lower sea level, especially during Pleistocene glacial intervals, portions of the Nicaraguan Plateau may have been emergent and in closer proximity to the Swan Islands than the mainland is at present, perhaps as close as 100 km.

The lack of evidence for land connection between the Swan Islands and either the Middle American mainland or any of the West Indian islands eliminates the geographic fragmentation and subsequent vicariance of an ancestral biota as a viable hypothesis for the origin of the Swan Islands fauna. Dispersal remains as the only explanation for the existence of a vertebrate fauna on the Swan Islands. Darlington (1937) noted that in the Greater Antilles most storm tracks, particularly hurricanes, and the prevailing trade winds come from the northeast, favoring dispersal of organisms from the Greater Antilles to the Swan Islands. Present-day currents, on the other hand, come out of the southeast; however, current patterns in the Caribbean may have been radically different prior to the connection of North and South America in the late Pliocene or early Pleistocene.

The vertebrate fauna of the Swan Islands consists of 18 species: nine reptiles,

eight birds, and one mammal. Table 2 lists the vertebrates known to breed in the Swan Islands and summarizes the general (mainland or West Indian) and specific zoogeographic affinities of each species. Additional indigenous species of vertebrates may be added with future collecting, although the likelihood of adding more than a few species is slight, considering the many naturalists who have collected in the Swan Islands (at least ten, based on the literature). The Swan Islands will be considered as a zoogeographic unit in my analysis despite several examples of anomalies in distribution between the islands, the most notable being the presence of *Geocapromys thoracatus* on Little Swan, but not on Great Swan.

The herpetofauna of the Swan Islands is entirely reptilian, consisting of seven lizards and two snakes (MacLean *et al.* 1977; Schwartz and Thomas 1975). Of these nine species, four have mainland affinities, four are derived from the West Indies, and one occurs in both regions. None of the species of mainland origin are represented by endemic subspecies, although subspecies of *Ameiva ameiva* and *Leptotyphlops goudoti* are restricted to the Swan Islands and one or more islands off the coast of Honduras and Nicaragua. In contrast, three of the four reptiles of West Indian origin have endemic subspecies in the Swan Islands and the fourth, *Leiocephalus carinatus varius,* occurs only in the Swan and Cayman Islands. Excluding sea birds, which are too widely distributed for zoogeographic analysis, only five species of land birds breed in the Swan Islands (Paynter 1956) and all are clearly derived from the West Indies. An endemic subspecies of *Dendroica vitellina* occurs in the Swan Islands, a species found elsewhere only in the Cayman Islands. *Geocapromys thoracatus* is the only mammal recorded from the Swan Islands, and it is also the only endemic species of vertebrate known from the two islands. The Swan Island Hutia has its closest affinities with the Jamaican species, *G. brownii.*

The land snail fauna of the Swan Islands provides an interesting comparison with the vertebrates. The land snails are more diverse than the vertebrates, represented by at least 22 species (Pilsbry 1930). Eight of these species are so widely distributed in the West Indies and Middle America that the origin of the Swan Island forms cannot be determined. Eleven species are conspecific with or related to West Indian forms, whereas only three species have been derived from the Middle American mainland. Furthermore, of the nine endemic species of land snails found in the Swan Islands, all but one are of West Indian origin. Pilsbry (1930) noted that the endemic land snails showed a special resemblance to forms from Jamaica and Grand Cayman, especially the latter.

The endemic nature of the West Indian complement of the vertebrate fauna, including one endemic species and four subspecies, together with the high endemism of the Swan Island land snails with West Indian affinities, suggests that this portion of the fauna has been isolated in the Swan Islands for a longer period of time than the species derived from the Middle American mainland. This assumes that evolutionary rates among Swan Island species have been constant and that the greater degree of morphological differentiation shown by the West Indian component of the fauna indicates a longer period of isolation. Since the Swan Islands lack a fossil record of terrestrial species, this hypothesis is not testable, nor does there appear to be a clear explanation for the supposedly greater antiquity of the West Indian forms. Even if the individual species have remained static in an evolutionary sense since becoming isolated on the Swan Islands, the endemic

forms, at least among the vertebrates, probably originated no earlier than the Pleistocene.

The zoogeographic data indicate that the Swan Islands vertebrate fauna, although small, is complex and has been derived from a diversity of sources, including Cuba, Jamaica, the Cayman Islands, the Caribbean coast of Middle America from the Yucatan Peninsula to Nicaragua, and several islands off the coast of Honduras and Nicaragua. More of the species (nine) share affinities with forms from the Cayman Islands than from any other single source area. Two generalized distributional patterns or tracks (sensu Rosen 1976) are evident from the zoogeographic data. The most important generalized track connects the Swan Islands with Cuba, Jamaica, and the Cayman Islands, accounting for 10 species (70%) of the vertebrates of known zoogeographic affinities. A smaller track, accounting for four species (30%), links the Swan Islands with the Middle American mainland. As discussed above, these distributional tracks are best explained by overwater dispersal rather than vicariance, the latter being falsifiable on geological grounds. Both Hershkovitz (1958) and Koopman (1959) placed the Swan Islands in the West Indian Subregion of the Neotropical Region based solely on the presence of *Geocapromys thoracatus*. Zoogeographic analysis of the remainder of the vertebrate fauna substantiates the placement of the Swan Islands in the West Indian Subregion.

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